The Production, Storage, and Flow of Carbon in Amazonian Forests

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The carbon stores and dynamics of tropical forests are the subject of major international scientific and policy attention. Research associated with the Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA) has generated substantial advances in our understanding of the cycling of carbon at selected forest sites in Brazilian Amazonia and generated new insights into how these processes may vary across the wider Amazonian region. Here we report on aspects of this new understanding. We present, in particular, a comprehensive synthesis of carbon cycling in three focal LBA sites (Manaus, Tapajós, and Caxiuanã), drawing on studies of productivity, litterfall, respiration, physiology, and ecosystem fluxes. These studies are placed in the context of the wider Amazonian region by utilizing the results of the Amazon Forest Inventory Network (RAINFOR) and other forest plots. We discuss the basin-wide distribution of forest biomass derived by combining these plots and a suite of satellite data, and examine the dynamics of carbon cycling in the context of regional carbon stores in the forest. Particular attention is drawn to the strong relationship between forest productivity and turnover, which suggests that higher levels of forest productivity increase forest dynamism rather than forest biomass. We conclude by discussing what the scientific priorities should be for a synthetic region-wide understanding of the carbon dynamics and stores of Amazonian forests.

1. INTRODUCTION

There is currently unprecedented interest in the carbon cycling and carbon storage of tropical forests, stimulated by a renewed global effort to limit rates of carbon dioxide emissions from deforestation as a strategy contributing to the mitigation of global atmospheric change, and also by a concern that climate change may result in net carbon emissions from tropical forests, and thus a positive feedback on climate change. Much of this interest is focused on assessing the magnitude of carbon stores in these forests, understanding what determines the magnitude of these stores and exploring how these stores will respond to either mitigate or accelerate climate change.

Amazonia is home to half of the world's tropical forests, yet until recently, there has been little detailed exploration of the carbon dynamics of its forests, nor the spatial variation of their carbon cycle. The Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA) program and associated research provided a unique opportunity to explore these issues, both through intensive studies at a number of sites, and from a Pan-Amazonian perspective of the role of Amazonia in the earth system.

In this chapter, we review and synthesize some recent advances that LBA-associated research has made in our understanding of the carbon cycling of Amazonian forests,

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focusing on three questions: (1) What synthetic picture do studies at key LBA study sites provide about stocks and flows of carbon at these sites? (2) How do these focal LBA sites fit into the wider context of Amazonian forests? (3) What does the relationship between carbon allocation, biomass production, and biomass stock tell us about spatial and temporal variations in carbon cycling and carbon storage in old-growth Amazonian forests?

To pursue these questions, we will draw on three main lines of research. First, we focus on a detailed synthesis of carbon cycling research at three LBA study sites (Manaus, Tapajós, and Caxiuanã; hereafter termed the "focal sites"), where there has been an overlap of forest mensuration and net primary productivity (NPP) studies, ecophysiological and respiration measurements, and eddy covariance studies of above-canopy fluxes. This synthesis is largely drawn from *Malhi et al.* [2009]; detailed analysis and discussion of the caveats of this synthesis are presented in that paper. Here we summarize the results of the synthesis without dwelling on methodological issues. Second, to put these sites into the wider context, we draw on forest plots and NPP studies across Amazonia from the Amazon Forest Inventory Network (RAINFOR) [*Malhi et al.*, 2001], in particular, studies of the spatial variation of productivity [*Malhi et al.*, 2004; *Aragão et al.*, 2009] and biomass [*Baker et al.*, 2004; *Malhi et al.*, 2006]. The temporal shifts in forest carbon dynamics observed in this network are discussed by *Phillips et al.* [this volume], and spatial relations to plant ecophysiology are discussed by *Lloyd et al.* [this volume]. Our focus here is on mean annual or longer-term budgets in the carbon cycle: we will not discuss seasonal or interannual variations (somewhat discussed by *Saleska et al.* [this volume]). Third, we also draw on and discuss the remote sensing-based approach to spatial extrapolation of biometry data, as employed by *Saatchi et al.* [2007].

The three focal study sites are situated on deep, highly weathered Oxisols in terra firme forests on upland areas of lowland eastern Amazonia. At Manaus and Caxiuanã, the Oxisol landscape is occasionally dissected by valleys with seasonally waterlogged Spodosols and a lower biomass forest, whereas the site at Tapajós sits on a broad plateau (~90 m above sea level) with little stream development. The majority of detailed process studies have focused on the Oxisol/terra firme landscape, whereas the flux tower footprint extends across a broader landscape of plateaus and river valleys. For further discussion of the sites, see *Malhi et al.* [2009]. We also report on new assessments of NPP at other sites, particularly in western Amazonia (Colombia and Peru), as reported by *Aragão et al.* [2009]. A summary of these sites is given in Table 1, and the sites are plotted in Figure 1.

Table 1. Site Codes, Locations, and Climatic Characteristics of the 10 Net Primary Productivity Amazonian Sites Reported in This Study Including the Three Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA) Focal Sites Caxiuanã, Manaus K34, and Tapajós km 67[a]

Study Sites					Climate		
Amazon Forest Inventory Network Sites Code			Location		Rainfall, mm a^{-1}	DSL, months	MAT, °C
	Name	Country	Latitude	Longitude			
AGP01	Agua Pudre plot E	Colombia	−3.72	−70.3	2723	0.0	25.5
AGP02	Agua Pudre plot U	Colombia	−3.73	−70.4	2723	0.0	25.5
CAX03	Caxiuana drought experiment control plot	Brazil	−1.72	−51.5	2314	4.0	26.9
CAX06	Caxiuana flux tower site LBA	Brazil	−1.72	−51.5	2314	4.0	26.9
CAX08	Caxiuana terra preta site	Brazil	−1.72	−51.5	2314	4.0	26.9
MAN05, MAN12, BNT04	Manaus K34 flux tower site LBA	Brazil	−2.5	−60.0	2272	3.0	27.1
TAM05	Tambopata RAINFOR plot 3	Peru	−12.8	−69.7	2417	3.5	25.2
TAM06	Tambopata RAINFOR plot 4	Peru	−12.9	−69.8	2417	3.5	25.2
TAP04	Tapajós km 67 flux tower site LBA	Brazil	−2.5	−55.0	1968	4.5	26.1
ZAR01	Zafire, Varillal	Colombia	−4.0	−69.9	2723	0.0	25.5

[a]The climate data presented in this table are mean values from 1960 to 1998 derived from the University of East Anglia Observational Climatology [*New et al.*, 1999] and published in the work of *Malhi et al.* [2004]. Cumulative annual rainfall is given in mm a^{-1}, dry season length (DSL) in months, corresponds to the sum of consecutive months with rainfall < 100 mm month^{-1}, and temperature is the mean annual temperature (MAT) in degrees Celsius. Modified from *Aragão et al.* [2009].
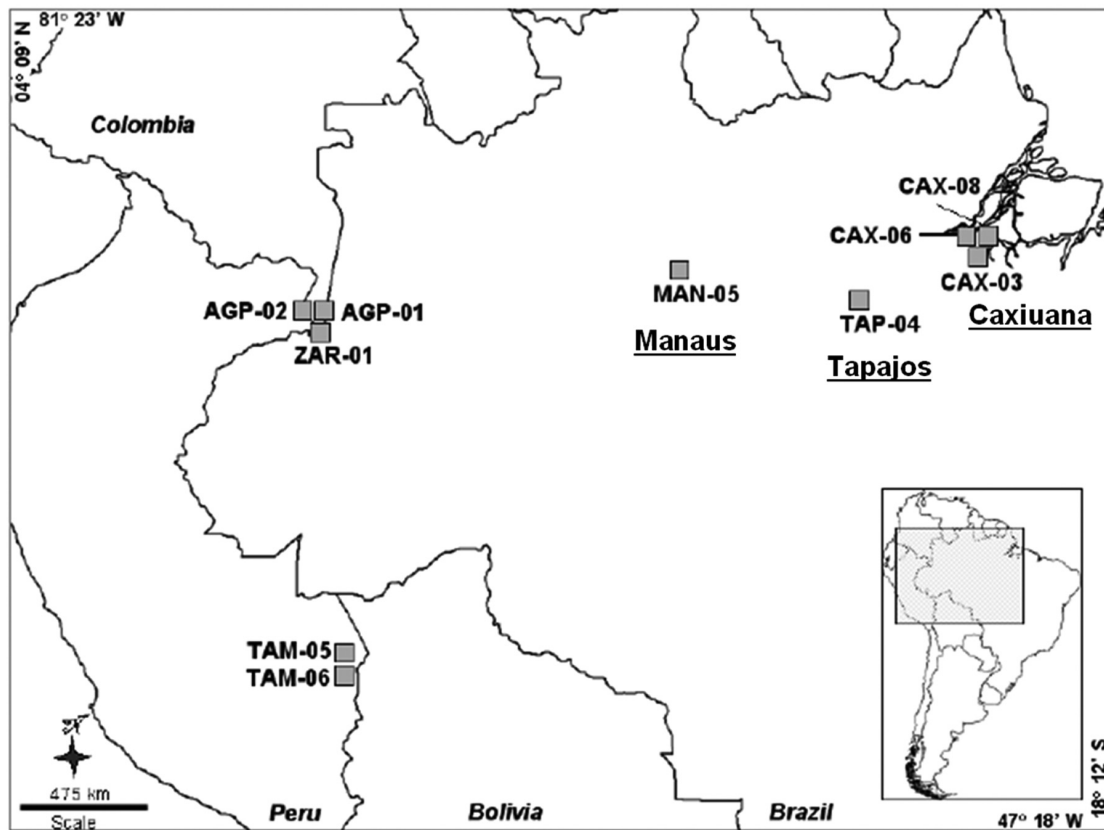
Figure 1. A map of the Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA) and Amazon Forest Inventory Network (RAINFOR) net primary productivity (NPP) sites mentioned in this chapter. The focal LBA sites (Manaus, Tapajós, and Caxiuanã) are underlined. Site codes are listed in Table 1. From *Aragão et al.* [2009].
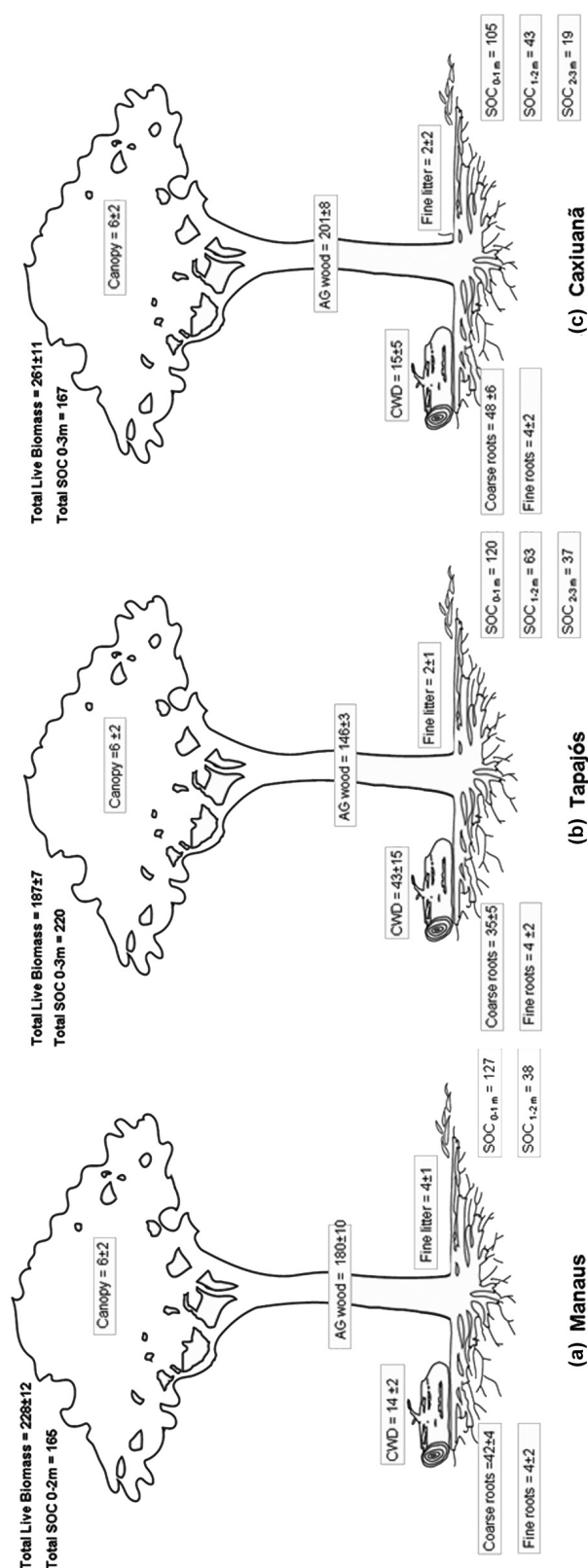
2. STOCKS OF CARBON

A synthesis of reported values of carbon stocks at each focal site is summarized in Figure 1. Detailed discussion of the data sets and the procedure employed to average across studies are presented by *Malhi et al.* [2009]. All carbon stocks are in Mg C ha^{-1}; 1 Mg C ha^{-1} is equal to 100 g C m^{-2}.

2.1. Aboveground Live Biomass

Aboveground (AG) live biomass is highest at Caxiuanã, slightly lower on the Manaus plateau, and lowest at Tapajós km 67 and in the Manaus valley bottoms. Some of these differences are reflected in forest structure: Caxiuanã has a greater proportion of large trees than Manaus. All these studies applied the allometric equation of *Chambers et al.* [2001], modified by species-specific densities as applied by *Baker et al.* [2004]. Hence, the differences between sites largely reflect structural differences rather than methodo-

logical ones. *Palace et al.* [2008] estimated tree density and size for seven sites in Amazonia, including the three focal sites in this chapter, with the same trend in tree density and tree size based on crown width (more trees per hectare, but smaller trees, in Manaus, in comparison with larger but less trees at Caxiuanã).

In the wider context of Amazonia, these focal sites tend to have higher-than-average biomass [*Baker et al.*, 2004; *Malhi et al.*, 2006]. Typical AG live biomass in these eastern Amazonian deep Oxisol forests is between 300 and 350 Mg dry weight ha^{-1} (Plate 2), equivalent to 150–175 Mg C ha^{-1}. Similar high biomass values are found in the Guyanas, but biomass tends to decline into the drier margins of Amazonia as wood volume declines (Figure 2). This decline probably occurs because seasonal drought intensifies the relative importance of root competition for water over crown competition for light, the median intertree spacing consequently increases, and the number of trunks per unit area declines. In contrast, biomass also tends to decline as one heads west,

Figure 2. (opposite) Carbon stocks in the aboveground (AG) and belowground (BG) compartments of the three focal LBA Amazonian forests. (a) Manaus, (b) Tapajós, (c) Caxiuanã. Units are in Mg C ha^{-1}.

irrespective of whether this is to dry southwestern Amazonia or wet northwestern Amazonia (Plate 2). This decline appears associated with an increase in wood productivity and a decrease in mean wood density (Plate 1). Hence, the high AG biomass in the eastern Amazonian focal sites appears driven largely by the influence of soils on forest structure and tree life-history traits. Infertile soils tend to favor slow growing, long-lived tree species, which invest more in herbivore and pathogen defense strategies such as high wood density. Mean wood density is about 15% higher in the eastern Amazonian RAINFOR sites than in western Amazonian sites [*Baker et al.*, 2004].

2.2. Aboveground Dead Biomass

AG coarse woody debris (CWD) has been measured at Manaus [*Chambers et al.*, 2004] and Tapajós, and is much greater at multiple sites across Tapajós. The CWD stocks at Tapajós appear to be in disequilibrium across a wider area [*Pyle et al.*, 2008] and in combination with the low AG biomass, this suggests that the Tapajós local region underwent a recent and widespread major disturbance, most likely in the 1990s [*Keller et al.*, 2004; *Pyle et al.*, 2008]. CWD has not been measured at Caxiuanã, but was estimated by taking estimates of mortality biomass inputs and dividing by a wood decay constant, k_{wood}, of 0.16 ± 0.04 (see below) [*Malhi et al.*, 2009], producing values very close to those observed at Manaus (15 ± 5 Mg C ha^{-1} a^{-1} versus 14 ± 2 Mg C ha^{-1} a^{-1}, respectively). This assumes near-equilibrium conditions, but at the Caxiuanã tower plot, there is little evidence of the numerous large fallen trees seen at Tapajós km 67 (Y. Malhi, personal observation). A recent unpublished CWD census for Caxiuanã (D. Metcalfe, unpublished data, 2008) confirms this estimate. Values of CWD at Tapajós are the highest reported for any site in lowland Amazonia [*Baker et al.*, 2007].

2.3. Belowground Biomass

Belowground (BG) biomass stocks are predominantly in the coarse roots of live trees, with fine roots being a very minor component of the stock (though a large component of the turnover; see below). Root biomass has rarely been measured by direct harvesting, except in the vicinity of Ma-

naus by *Klinge* [1973] and more recently by N. Higuchi et al. (unpublished data, 2008). Estimates based on soil cores or pits tend to underestimate biomass by being forced to exclude the core root areas immediately underneath trees. In the absence of direct excavation, the best estimate of BG biomass may come from generalized empirical ratios for tropical rainforests: *Malhi et al.* [2009] estimated root biomass by multiplying the AG biomass values for the plateaus by a root:shoot ratio of 0.21 ± 0.03, encompassing the values reported for the tropics in the global surveys of *Jackson et al.* [1996] and *Cairns et al.* [1997]. A similar value of 0.21 has been confirmed by extensive and comprehensive BG biomass sampling of 131 trees in the vicinity of the Biomassa e Nutrientes na Floresta Tropical (BIONTE) plots near Manaus (N. Higuchi et al., unpublished data, 2008).

There is very little information on likely regional-scale variation in root biomass. Root biomass would be expected to be low in shallow soils (as may occur in crystalline shield regions or on montane slopes), soils with impermeable and shallow hardpans, or where they are limited by anoxia associated with seasonally high water tables, as are extensive in the broad poorly drained landscape between Manaus and the Andes foothills. Given suitable soils, the proportion of biomass in roots may be greater in seasonally drier forests and is known to be much greater in cerrado and cerradão regions, where more than 71% of total live biomass can be BG [*Castro and Kaufmann*, 1998].

2.4. Soil Carbon

Soil carbon (C) stocks are usually reported only for the top 30 cm or top 1 m of soil, and range between 74 and 127 Mg C ha^{-1} for studies in our focal sites. Quesada reports (reported by *Malhi et. al*. [2009]) C stocks for all three sites to 2 m depth, showing substantial C stocks at these depths and evidence for further carbon storage at greater depths, particularly at Tapajós.

2.5. Total Carbon Storage

Total AG C stocks are similar at all three sites (Manaus 199, Tapajós 202, Caxiuanã, 231 Mg C ha^{-1}), with the smaller amount of biomass in living vegetation at Tapajós compensated by the higher CWD. Total carbon stocks to 2 m depth are presented in Figure 2 from *Malhi et al.* [2009]; data were derived from *Quesada et al.* [2009]. BG C stocks to 2 m depth are very similar in magnitude to AG stocks, with Tapajós showing the highest soil carbon stocks. Total C stocks (to 2 m depth) are 406 Mg C ha^{-1} at Manaus, 422 Mg C ha^{-1} at Tapajós, and 427 Mg C ha^{-1} at Caxiuanã. These values would certainly increase if greater soil depths

are considered and would be much lower for Manaus if the full plateau-valley landscape was considered. Overall, as much C is stored BG as AG, overwhelmingly in the soil carbon pool. How important these stocks are when considering the carbon value of rainforests depends on how vulnerable they are following land use change. Conversion to cattle ranching has little impact on soil C stocks, whereas intensive ploughing-associated agriculture may substantially oxidize carbon stocks in the upper soil layers.

3. NET PRIMARY PRODUCTIVITY AND ITS COMPONENTS

The NPP, the net amount of carbon fixed per unit time into organic matter, is a fundamental property predicted by many ecosystem models and a metric of resource use by ecosystems. Comprehensive measurements of NPP have been rare in tropical forests [*Clark et al*., 2001a; *Chambers et al*., 2004], with most studies reporting only wood productivity or total AG productivity (woody production plus fine litterfall). The intensity of effort at the focal LBA sites provides an opportunity for a more comprehensive assessment of NPP, putting component measurements into context. *Malhi et al.* [2009] examined and synthesized the studies of NPP components at the focal sites, including an analysis of uncertainty and self-consistency, and discussion of caveats. Synthesized values of NPP (and respiration) for the LBA focal sites are illustrated in Figure 3, and for ten RAINFOR sites, the components of AG and BG NPP are plotted in Figure 4 [from *Aragão et al.*, 2009]. We discuss each of the major terms in turn.

3.1. Woody Biomass Productivity

AG wood productivity, NPP$_{stem}$, is the most visible aspect of forest productivity and can be measured by recensus of tree diameters and new recruits. General allometric relationships [e.g., *Chambers et al.*, 2001; *Chave et al*., 2005] are then employed to convert these estimates to changes in woody biomass, and the changes of these terms per unit time are summed over individual trees and then used to estimate total AG productivity, with some correction for the fraction of trees missed between censuses [*Malhi et al.*, 2004]. All values reported here employ the *Chambers et al.* [2001] allometry, as modified by *Baker et al.* [2004] to incorporate wood density where wood density values were given. The alternative widely employed tropical allometric equation from *Chave et al*. [2005] seems to overestimate the biomass of large Amazonian trees [*Pyle et al.*, 2008]. As defined here, NPP$_{stem}$ includes the net woody production of the tree crown associated with changes in tree size and form, but excludes

any turnover and replacement of crown branches (this term, NPP_{branch} is discussed below).

NPP_{stem} at the Manaus and Caxiuanã plots ranges between 2.0 and 2.9 Mg C a^{-1}, values that are typical of eastern Amazonian forests [*Malhi et al.*, 2004]. Tapajós tends to show higher wood productivity over a wide area, particularly in the larger-scale censuses [*Pyle et al.*, 2008]. As indicated above, this appears to be correlated with high CWD, indicating a large-scale disturbance event in the Tapajós region in recent years.

The values at Manaus and Caxiuanã are among the lower values of NPP_{stem} reported for Amazonian forests [*Malhi et al.*, 2004] (Figure 4). Wood productivity shows a distinctive regional trend across Amazonia, with highest values found in western Amazonia, both in the wet northwest and in the seasonally dry southwest. The values at the eastern site of Tapajós, however, compare with the high values found in western Amazonia. The generally higher values across western Amazonia irrespective of rainfall suggest that climate is not the major factor in determining wood productivity. Instead, soils seem to exert more influence, most likely through the supply of phosphorus [*Davidson et al.*, 2007], and there is a general trend of increasing wood productivity with increasing soil fertility and specifically soil phosphorus [*Malhi et al.*, 2004; *Quesada et al.*, 2009; *Aragão et al.*, 2009]. Lowland forest soils in western Amazonia tend to be less infertile, being typically of Pleistocene or Holocene age and initiated by meandering rivers depositing sediment eroded from the Andes. The lowest values of NPP_{stem} are found on white sand soils in the upper Rio Negro region (northwest Amazonia). Soils in lowland eastern Amazonia have generally been weathered, eroded, and re-deposited over a much longer timescale than those in western Amazonia.

3.2. Canopy Productivity

The NPP of the canopy, NPP_{canopy}, is the annual rate of net fixation of carbon into the structures of leaves, flowers, fruit, and (for methodological convenience) small twigs (typically <1 cm diameter). For a near-equilibrium forest, its annual value can be measured through an array of litter traps collected at frequent (e.g., biweekly) intervals to minimize decomposition [*Clark et al.*, 2001b]. Productivity estimates based on litterfall rely on the assumption that the litterfall is approximately equal to productivity of that component. This assumption is weaker if interannual variability is significant, especially for larger components such as branches, and is also complicated by the trapping and in situ decomposition of dead material in the canopy. Measurements are also challenged if the spatial pattern of litterfall is aggregated rather than a uniform "rain" of litter.

For Caxiuanã and Manaus, fine litterfall values average 3.6–3.8 Mg C ha^{-1} a^{-1} (Figure 3). Tapajós is again an exception, with higher mean values approximately in proportion to the higher wood productivity. At Caxiuanã, 73% of the litter was from leaves, 12% from flowers and fruit, 8% twigs, and 7% unidentifiable (Almeida and L. E. O. C. Aragão, unpublished data, 2008).

In the context of the wider Neotropics, *Malhi et al.* [2004] reported a fairly strong linear relationship, between NPP_{litter} and NPP_{stem} (this analysis included older data from the two focal sites Caxiuanã and Manaus), with the highest value reported being from Barro Colorado Island in Panamá. The newer data from the 10 Amazonian NPP sites are consistent with this relationship (Figure 5). The lower wood productivity at Caxiuanã and Manaus is reflected in lower canopy productivity, whereas both wood and canopy productivity at Tapajós are among the highest reported in Neotropical forests, even when compared with the productive sites of western Amazonia or the fertile terra preta site.

3.3. Coarse Woody Litterfall

Coarse woody litterfall can be an important component of forest carbon cycling, but is notoriously difficult to measure. It can be divided into three components: trunk mortality, nonlethal large branch shedding, and twig and small branch fall (pieces between 1 cm and 10 cm diameter). The division from fine litterfall is often set at 1 cm diameter for twigs. This division is largely for methodological convenience: small branches are too heterogeneous in placement and too large to be adequately captured by fine litter traps.

Trunk mortality, D_{stem}, should be close to wood productivity for quasi-equilibrium forests, although for many plots, it has been reported to be slightly lower, resulting in a slight net AG biomass increment over time. Branch loss rates have been reported for Manaus and Tapajós [*Chambers et al.*, 2001; *Nepstad et al.*, 2002; *Palace et al.*, 2008], and have a typical value of 1 ± 1 Mg C ha^{-1} a^{-1} [*Malhi et al.*, 2009]. This is an approximate measure of branch turnover, NPP_{branch} (but see discussion by *Malhi et al.* [2004]) and is added to the total estimate of AG NPP.

3.4. Volatile Organic Compound Emissions

The emission of volatile organic compounds (VOCs) from vegetation is a source of carbon from the vegetation, and can play an important role in local and regional atmospheric chemistry [see *Kesselmeier et al.*, this volume]. For the K34 tower near Manaus, *Kuhn et al.* [2007] report a total 24-h VOC flux (isoprene plus monoterpenes) of 24 Mg C m^{-2} day^{-1} for the period 17–25 July 2001, which if fairly invari-
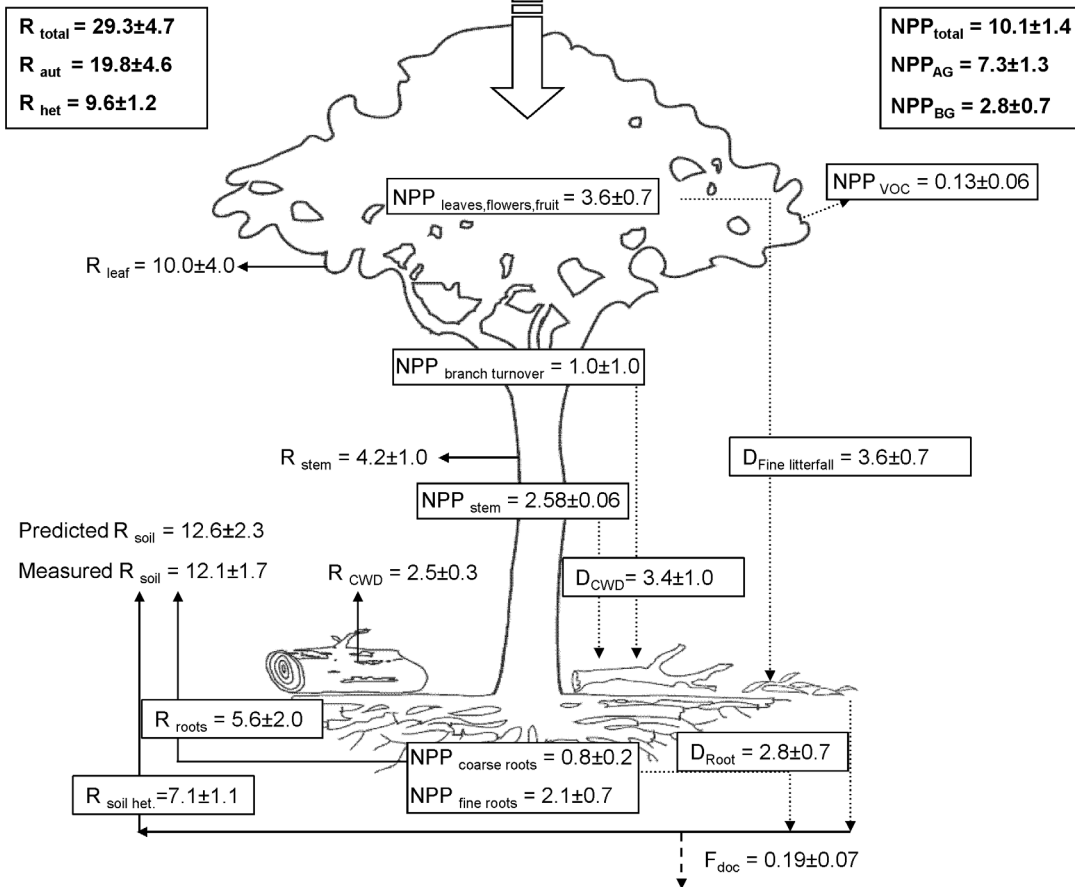
Figure 3. Components of forest productivity of the three focal LBA Amazonian forests. (a) Manaus, (b) Tapajós, (c) Caxiuanã. Units are in Mg C ha^{-1} a^{-1}. The diagram shows the partitioning of the gross primary productivity into components of NPP$_{total}$ and autotrophic respiration.

ant over the year is equivalent to an annual total of 0.088 Mg C ha^{-1} a^{-1}. Similar values were reported by *Greenberg et al.* [2004] at Tapajós and by previous studies north of Manaus (summarized by *Kuhn et al.* [2007]). In carbon terms alone, the VOC flux is clearly a small component of the internal carbon cycle, and for our synthesis, we allocate a value of 0.1 ± 0.05 Mg C ha^{-1} a^{-1} for all three focal sites.

Methane emissions from terra firme tropical forests are a new subject of interest, but still controversial. *do Carmo et al.* [2006] applied a canopy budget model to measured soil-atmosphere fluxes of methane to estimate net methane emissions from upland forests of 2–21 Mg CH$_4$ m^{-2} d^{-1}, equivalent to 0.005–0.06 Mg C ha^{-1} a^{-1}. Taking the midrange, *Malhi et al.* [2009] allocate 0.03 ± 0.03 Mg C ha^{-1} a^{-1} to methane emissions. Combining these with the estimate of isoprene and monoterpene emissions, they arrive at an estimate of total volatile emissions of 0.13 ± 0.06 Mg C ha^{-1} a^{-1}.

3.5. Fine Root Productivity

Two major components in BG productivity, D_{root}, are coarse root productivity and fine root productivity. A third component is the export of organic material in the form of exudates, or to symbionts such as mycorrhizal fungae and nitrogen-fixing bacteria. This third term is hard to quantify and is often treated as part of rhizosphere respiration (e.g., exudate that is rapidly metabolized is, for many practical purposes, indistinguishable from root respiration).

Fine root productivity is defined as the production of root material less than a threshold diameter, usually 2 mm. The value calculated for fine root production can depend on
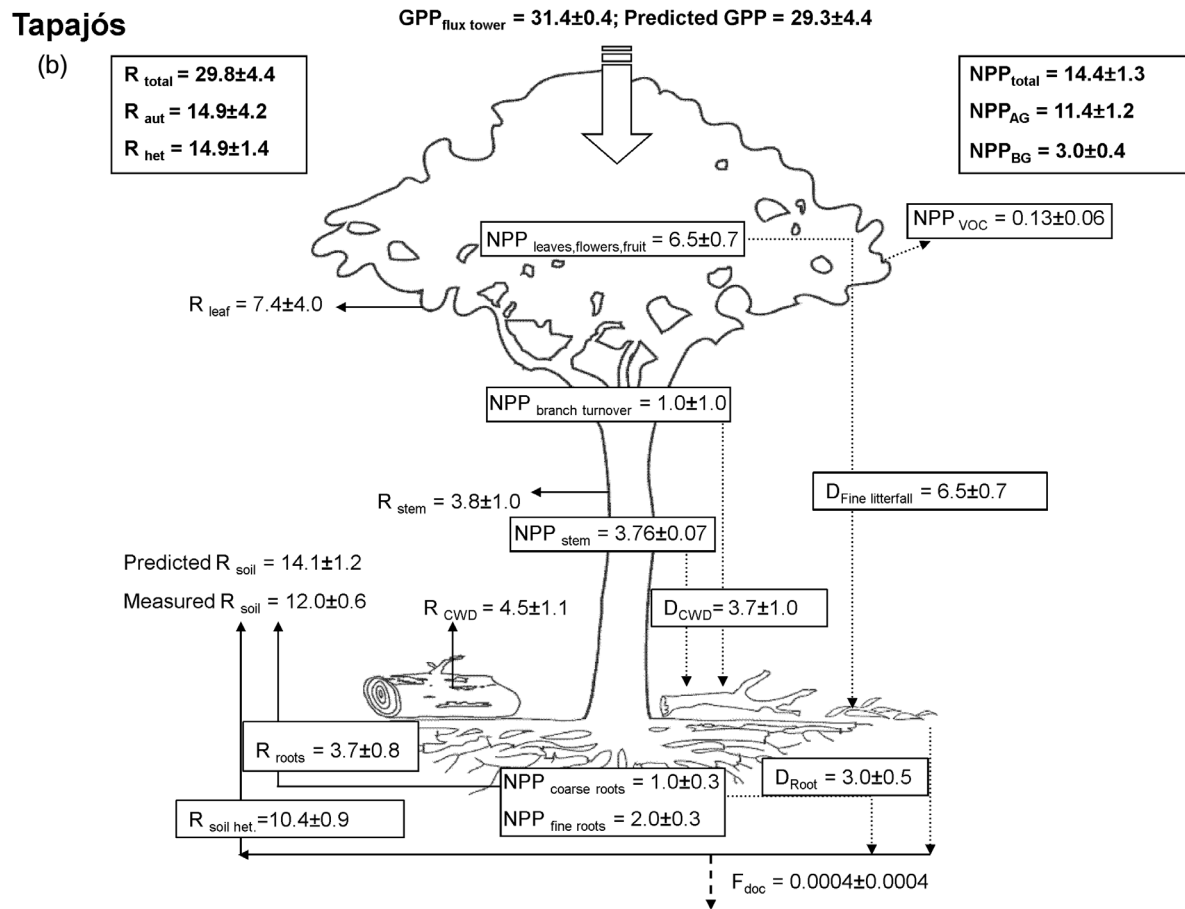
Tapajós

(b)

$GPP_{flux\ tower} = 31.4\pm0.4$; Predicted GPP = 29.3 ± 4.4

$R_{total} = 29.8\pm4.4$

$R_{aut} = 14.9\pm4.2$

$R_{het} = 14.9\pm1.4$

$NPP_{total} = 14.4\pm1.3$

$NPP_{AG} = 11.4\pm1.2$

$NPP_{BG} = 3.0\pm0.4$

$NPP_{leaves,flowers,fruit} = 6.5\pm0.7$

$NPP_{VOC} = 0.13\pm0.06$

$R_{leaf} = 7.4\pm4.0$

$NPP_{branch\ turnover} = 1.0\pm1.0$

$R_{stem} = 3.8\pm1.0$

$D_{Fine\ litterfall} = 6.5\pm0.7$

$NPP_{stem} = 3.76\pm0.07$

Predicted $R_{soil} = 14.1\pm1.2$

Measured $R_{soil} = 12.0\pm0.6$

$R_{CWD} = 4.5\pm1.1$

$D_{CWD} = 3.7\pm1.0$

$R_{roots} = 3.7\pm0.8$

$D_{Root} = 3.0\pm0.5$

$R_{soil\ het.} = 10.4\pm0.9$

$NPP_{coarse\ roots} = 1.0\pm0.3$

$NPP_{fine\ roots} = 2.0\pm0.3$

$F_{doc} = 0.0004\pm0.0004$

Figure 3b. (continued)

sampling methodology, in particular, the technique employed and the depth to which the soil is sampled. Fine root production values have been reported for Caxiuanã and Tapajós. For Caxiuanã, rhizotron and ingrowth core methods were used to 30 cm [*Metcalfe et al.*, 2007b]; for Tapajós, a combination of sequential coring and root trenching were employed [*Silver et al.*, 2000]. An important discrepancy between these two studies is the depth to which root production is measured, 30 cm at Caxiuanã versus 10 cm at Tapajós. *Malhi et al.* [2009] attempt to correct for this discrepancy by using root profiles to standardize to 1 m depth. Once this is done, there is no significant difference in estimates of fine root productivity between the two sites (Caxiuanã, 2.2 ± 0.6 Mg C ha^{-1} a^{-1}; Tapajós, 2.0 ± 0.3 Mg C ha^{-1} a^{-1}). For Manaus, no data were available, and we take the mean of the Caxiuanã and Tapajós values, with conservative error bars of ±1.0 Mg C ha^{-1} a^{-1}. At the RAINFOR NPP sites, root productivity was estimated from ingrowth cores as reported by *Aragão et al.* [2009].

The resulting values are shown in Figures 3 and 4.

3.6. Coarse Root Productivity

Coarse root productivity is the productivity of larger, more lignified roots. These can be divided into roots <10 cm diameter, which can be expected to be reasonably homogeneous in distribution and amenable to conventional random or grid-based sampling, and massive structural roots, which are very difficult to assess for biomass without excavation, and even more difficult to monitor over time. For massive structural roots, the best approach may be to assume that wood production per unit biomass is the same as for AG woody biomass and use the estimate of BG biomass being $21 \pm 3\%$ of AG biomass (see carbon stocks section above). When added to estimates of fine litterfall above, this yields values of total BG NPP of 2.9 ± 0.6 Mg C ha^{-1} a^{-1} (Caxiuanã), 2.8 ± 0.7 Mg C ha^{-1} a^{-1} (Manaus), and 3.0 ± 0.5 Mg C ha^{-1} a^{-1} (Tapajós).

Caxiuanã

(c)

GPP$_{flux\,tower}$ = 38.2±2.0; GPP$_{ecophysiology}$=31.2; Predicted GPP = 31.4±4.4

R$_{total}$= 30.8±4.2
R$_{aut}$ = 21.4±4.1
R$_{het}$ = 9.4±0.8

NPP$_{total}$ = 10.0±1.2
NPP$_{AG}$ = 7.2±1.1
NPP$_{BG}$ = 2.8±0.6

NPP$_{leaves,flowers,fruit}$ = 3.8±0.1

NPP$_{VOC}$ = 0.13±0.06

R$_{leaf}$ = 8.9±4.0

NPP$_{branch\,turnover}$ = 1.0±1.0

R$_{stem}$ = 5.1±0.5

D$_{Fine\,litterfall}$ = 3.8±0.1

NPP$_{stem}$ = 2.16±0.55

Predicted R$_{soil}$ = 14.6±0.9

Measured R$_{soil}$ = 13.5±0.9

R$_{CWD}$ = 2.2±0.4

D$_{CWD}$= 2.9±1.0

R$_{roots}$ = 7.4±0.5

D$_{Root}$ = 2.9±0.6

R$_{soil\,het.}$ = 7.2±0.8

NPP$_{coarse\,roots}$ = 0.7±0.2
NPP$_{fine\,roots}$ = 2.2±0.6

F$_{doc}$ = 0.19±0.07

Figure 3c. (continued)

3.7. Dissolved Organic Carbon Leakage

The possibility of waterborne carbon disappearing laterally through either surface runoff or groundwater slow into streams has been invoked as a possible reason for apparent carbon sinks in eddy covariance studies and as a partial source of the high CO_2 respired by rivers [*Richey et al.*, 2002; see also *Richey et al.*, this volume]. *Waterloo et al.* [2006] measured dissolved organic carbon (DOC) runoff in the Igarapé Açu catchment, which covers an area of 6.8 km², including the Manaus K34 micrometeorological tower.

Net carbon exports over 2 years (2002 and 2003) amounted to 0.19 ± 0.07 Mg C ha^{-1} a^{-1}. Almost all of this export seemed to originate in the riparian zone of the valley bottoms, which cover 35% of the watershed area in the local landscape. For plateau regions, the total DOC exports through groundwater seemed to be much less, around 0.0005 Mg C ha^{-1} a^{-1}. In

the same study, DOC concentrations in rainfall were 1.2 mg l^{-1}, resulting in annual DOC deposition rates in dissolved rainwater of 0.03 Mg C ha^{-1} a^{-1}. A significant proportion of DOC inputs are probably derived from scavenging of aerosols during rainfall formation and dry deposition. Dissolved inorganic carbon was not reported but is unlikely to be much greater in magnitude.

For their synthesis, *Malhi et al.* [2009] applied the values of DOC transfer reported from the Igarapé Açu catchment for Caxiuanã and Manaus. The Tapajós site is a plateau cut by few rivers, so they employed the values for only plateaus reported by Waterloo. They report net DOC export (DOC runoff − DOC deposition). In all cases, DOC transfer is clearly a very small component of the forest carbon cycle. The figures for the Açu catchment are comparable with the annual average carbon export for the Rio Negro basin over 1982–1984 of 0.126 Mg C ha^{-1} a^{-1} [*Richey et al.*, 1990], suggesting that broadly similar processes operate across the
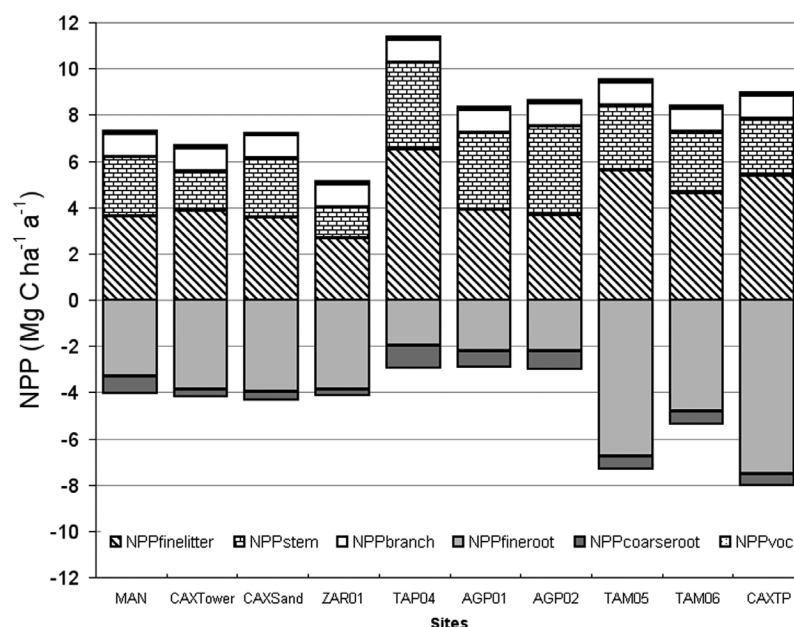
Figure 4. The components of NPP at the RAINFOR NPP sites, plotted in sequence of increasing soil phosphorus from left to right. Units are in Mg C ha^{-1} a^{-1}. BG NPP values are plotted as negative. From *Aragão et al.* [2009].

Amazon Basin, although there is likely to be local variation according to soil type and precipitation regime.

4. RESPIRATION FLUXES

Next, we turn our attention to the efflux of gaseous CO_2 from the system. This is termed "respiration" and can be divided into two terms, "autotrophic respiration" (CO_2 directly respired by plants as a breakdown product from their own metabolic activity), and "heterotrophic respiration" (CO_2 respired by herbivores, detritivores, and higher trophic levels as they consume and break down organic matter). In terms of the carbon cycle, the respiration is often conceived as a loss term (net carbon gain = photosynthetic input − respiratory loss), but this can be misleading. Respiration rates reflect the (usually efficient) allocation of metabolic activity of the plant or heterotrophic communities, whether to stem growth, leaf, or root tissue construction, protein maintenance, or reproduction. Plants or ecosystems that respire a smaller fraction of their fixed carbon are not necessarily any more "efficient," they are simply prioritizing other activities than biomass construction.

The ratio between NPP and autotrophic respiration reflects partitioning of the energy captured in plant photosynthesis [the gross primary productivity (GPP)] between construction of new organic material and work done in metabolic activity:

$$GPP = NPP + R_{autotrophic}.$$

Similarly, the ratio between autotrophic and heterotrophic respiration reflects the relative amount of metabolic activity occurring at the lowest trophic level (the plants and photosynthesizing bacteria) and in the sum of all other trophic levels (animals, fungi, bacteria).

4.1. Root Respiration

The partitioning of soil respiration into autotrophic (root) and heterotrophic respiration is helpful in terms of interpreting processes, but presents numerous methodological challenges [*Baggs*, 2006]. *Malhi et al.* [2009] report on measurements from Caxiuanã and Manaus.

At Caxiuanã, *Metcalfe et al.* [2007a] applied the direct extraction approach. *Silver et al.* [2005] quantified root respiration at Tapajós using two approaches: (1) a trenching experiment around a 2.5 m × 2.5 m block of land to 1 m depth, (2) a steady state mass balance approach based on quantifying AG and BG litter input, assuming that heterotrophic respiration rates are equal to litter input rates, and allocating the remaining soil respiration to root respiration. The trenching approach had varied success: here only results from the mass balance approach are reported.

There is a factor of two difference between the *Silver et al.* [2005] and *Metcalfe et al.* [2007a] estimates (Figure 2). This
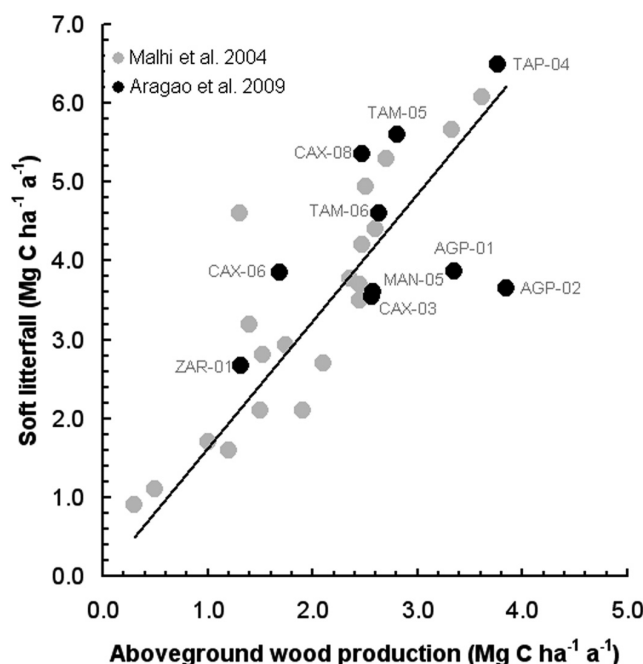
Figure 5. The relationship between the AG wood carbon production and the total litterfall production, both in Mg C ha^{-1} a^{-1}. Gray dots are values from across the Neotropics reported by *Malhi et al.* [2004], black dots are the 10 sites presented here. The linear fit (black line) incorporated all points and was forced through the origin, yielding a relationship, NPP$_{finelitter}$ = 1.61($\pm$0.07) $\times$ NPP$_{stem}$. From *Aragão et al.* [2009].

could reflect (1) genuine between-site differences, (2) an overestimation of root respiration by the extraction method at Caxiuanã, (3) an overestimation of heterotrophic respiration by the trenching and mass balance approaches. Details are discussed by *Malhi et al.* [2009].

For Manaus, we have no direct data and take the mean of the Caxiuanã and Tapajós values, with conservative error bars of $\pm$2 Mg C ha^{-1} a^{-1} to encompass the mean values of both other sites. For further review of soil and root carbon dynamics, see *Trumbore and de Camargo* [this volume].

4.2. Stem Respiration

The respiration of carbon dioxide from stems reflects the metabolic activity of stem maintenance and growth (and possibly some efflux of CO_2 carried in the stem water stream). Stem respiration has been measured at all three sites [*Chambers et al.*, 2004; *Nepstad et al.*, 2002; Teixeira et al., unpublished data, 2008]. Per unit stem area, the respiration rates were 0.6 μmol m^{-2} at Manaus and Tapajós and 0.78 μmol

m^{-2} at Caxiuanã. When these are scaled by the Stem Area Index for trees >10 cm diameter at breast height (calculated using the formula shown by *Chambers et al.* [2004]), the per unit ground area fluxes are 4.2 $\pm$ 1.0 Mg C ha^{-1} a^{-1}, 3.8 $\pm$ 1.0 Mg C ha^{-1} a^{-1}, 5.1 $\pm$ 0.5 Mg C ha^{-1} a^{-1}, respectively.

Similar values were reported by *Meir and Grace* [2002]: a mean value of ~0.6 μmol m^{-2} stem area s^{-1} for 23 species at Jarú, Rondônia, Brazil. *Yoda* [1983] reported that stem respiration rates increase with height along the tree; hence, the branch respiration estimate of *Chambers et al.* [2004] is probably low. More recently, *Cavaleri et al.* [2006] reported that, at La Selva, Costa Rica, per unit area respiration rates are much higher in branches than on the main trunk. This suggests that our estimates may be biased to being too low, although the total stem respiration reported at La Selva (5.08 $\pm$ 1.35 Mg C ha^{-1} a^{-1}) is not very different from that reported at these Amazonian sites.

4.3. Leaf Respiration

The respiration of leaves is a major plant metabolic activity, but is complicated by a number of definition and measurement issues. The first issue is to distinguish between photorespiration, the release of some CO_2 mediated by Rubisco and an intrinsic part of plant photosynthetic processes, and mitochondrial ("dark") respiration, which reflects the metabolic activity in the plant liberating energy utilized for plant maintenance and growth. In a diurnal cycle, mitochondrial respiration would be expected to increase with leaf temperature (and the amplitude of the diurnal cycle varies considerably within the canopy according to leaf position and sun and wind exposure), but can also decrease strongly with increasing solar radiation [*Atkin et al.*, 2000]. This decrease occurs because photosynthesis becomes a direct provider of adenosine triphosphate (ATP) for plant metabolic processes, reducing the demand for this from mitochondria.

The approach we adopt here is to attempt to estimate daytime photoinhibition and, hence, arrive at a total leaf dark respiration term that incorporates all leaf mitochondrial activity. An alternative approach that is sometimes adopted [e.g., *Litton et al.*, 2007] is to focus only on nighttime dark respiration [e.g., *Meir et al.*, 2008; *Lloyd et al.*, 2002] and ignore daytime dark respiration. We apply a 67% reduction of measured daytime dark respiration rates to allow for daytime photoinhibition, based on the *Atkin et al.* [2000] photoinhibition equations. Details of measurements and corrections are discussed by *Malhi et al.* [2009].

At Manaus, we estimate a leaf respiration rate of 10.0 Mg C ha^{-1} a^{-1} modified from data reported by *Chambers et al.* [2004]; at Tapajós, 7.4 Mg C ha^{-1} a^{-1} modified from data reported by *Domingues et al.* [2005] and at Caxiuanã, 8.9 $\pm$

1.4 Mg C ha^{-1} a^{-1}, derived from L. E. O. C. Aragão et al. (unpublished data, 2008).

In summary, leaf respiration is probably the largest single term in the internal carbon budget, but determination of its exact magnitude remains complex. The estimated sampling uncertainty for Caxiuanã (±1.4 Mg C ha^{-1} a^{-1}) does not account for potential systematic uncertainties in process and scaling, and for their synthesis table, *Malhi et al.* [2009] applied a more conservative uncertainty estimate of ±4.0 Mg C ha^{-1} a^{-1} to all three focal LBA sites.

5. ECOSYSTEM PHOTOSYNTHESIS AND RESPIRATION

Above-canopy eddy covariance studies attempt to measure the net carbon flux or net ecosystem exchange (NEE) in and out of the forest canopy [see *Saleska et al.*, this volume] and, hence, enable the estimation of ecosystem GPP and ecosystem respiration (R_e), by consideration of amplitude of the diurnal cycle of net carbon flux as outlined by *Reichstein et al.* [2005]. The method relies on assuming that nighttime flux data (or an appropriately filtered subset of these data) are reliable and extrapolating into the daytime (usually on the basis of temperature) to estimate daytime respiration. The difference between measured net carbon uptake and the estimated ecosystem respiration (which is in the opposite direction) is then the estimated gross primary production. The major uncertainties in this approach are (1) the estimation of nighttime ecosystem respiration fluxes, which are highly problematic in calm tropical conditions, particularly within tall canopies, which decouple subcanopy air from above-canopy turbulence; (2) the assumptions behind extrapolation into daytime, in particular, which measurement of temperature to use and how to account for photoinhibition of leaf respiration. Once ecosystem respiration has be estimated, GPP can be calculated as:

$$GPP = R_e - NEE,$$

where a negative NEE indicates a net carbon flux into the forest canopy. Reported estimates of GPP are summarized in Figure 3.

6. A COMPREHENSIVE VIEW OF THE FOREST CARBON CYCLE AT THE LBA FOCAL SITES

The values of NPP and respiration distilled from the three focal LBA study sites are displayed in Figures 2 and 3.

Considering the components of net primary production first (Figure 3), the NPP at Manaus and Caxiuanã is similar (10.1 ± 1.4 Mg C ha^{-1} a^{-1} and 10.0 ± 1.2 Mg C ha^{-1} a^{-1},

respectively) and significantly higher at Tapajós (14.4 ± 1.3 Mg C ha^{-1} a^{-1}). The largest components of NPP are leaf/flower/fruit/twig production, followed by stem production. There is little evidence of any significant variation in BG NPP between the three LBA sites (though estimated fine root turnover at Manaus is simply an average of the other two sites). Hence, the high NPP at Tapajós is entirely explained by a disproportionate allocation to AG wood and foliar production. Once other sites across Amazonia are considered (Figure 4), it seems that BG NPP tends to increases almost in step with AG NPP, as soil fertility increases. Hence, disturbance appears to shift allocation AG, as trees compete for light in newly created gaps, whereas fertility does not appear to cause as large a shift in allocation.

The components of autotrophic respiration are much more challenging to quantify and the largest source of uncertainty in our calculations. Total estimates of autotrophic respiration are 19.8 ± 4.6 Mg C ha^{-1} a^{-1} (Manaus), 14.9 ± 4.2 Mg C ha^{-1} a^{-1} (Tapajós), and 21.4 ± 4.1 Mg C ha^{-1} a^{-1} (Caxiuanã). Leaf respiration is the largest component and the most uncertain. There are considerable methodological differences between sites in measurements of leaf and root respiration [outlined in *Malhi et al.*, 2009] that may explain some of the difference between sites.

Such comprehensive measurements of carbon cycling at these sites enable two independent checks of self-consistency. First, we can compare against measurements of soil respiratory CO_2 efflux [*Malhi et al.*, 2009]. The expected soil respiration can be calculated from rates of carbon inflow into the soil.

$$R_{\text{soil, expected}} = R_{\text{root}} + R_{\text{SOM}}.$$

If we assume quasi-equilibrium conditions on an annual time scale and negligible interannual variability, the heterotrophic respiration is:

$$R_{\text{SOM}} = NPP_{\text{fineroot}} + NPP_{\text{finelitter}} + F_{\text{(cw-soil)}} \cdot (NPP_{\text{trunk}} + NPP_{\text{branch}}) + NPP_{BG} - \Delta C - F_{\text{doc}},$$

where $F_{\text{(cw-soil)}}$ is the fraction of CWD that is transferred to the soil estimated as 0.24 ± 0.15 [*Malhi et al.* 2009], $F_{\text{(cw-soil)}}$ is the BG root biomass fraction (estimated as 0.21 ± 0.03; see above), and ΔC is the change in soil carbon stocks. We assume there is negligible change in soil carbon stocks, (i.e., $\Delta C \ll R_{\text{soil}}$), an assumption supported at Tapajós by radiocarbon studies [*Telles et al.*, 2003], and the resulting calculations of expected R_{soil} are shown in Figure 3. The largest contributors to soil respiration are fine litter, which is fairly

well-quantified, and root respiration, which carries greater methodological uncertainty. The material derived from CWD component is relatively minor, and hence, assumptions about the exact value of $F_{(cw-soil)}$ are not particularly important. When expected soil respiration is compared to measured soil respiration (Figure 3); there is a high consistency between approaches, increasing confidence that our understanding of the bulk flows of the BG carbon cycle at these sites is fairly complete (although there are many details in the processes and their sensitivities to environmental factors that are still to be understood). Agreement is particularly good at Manaus, but at the other two sites, there is some suggestion that less respiration is being measured than expected.

As a second cross-check, we can calculate GPP from bottom-up measurements with those estimated from flux towers. The GPP of the forest is by definition the sum of NPP and autotrophic respiration:

$$GPP = NPP + R_{autotrophic}.$$

These predicted values of GPP for the focal sites are 29.9 ± 4.8 Mg C ha^{-1} a^{-1} (Manaus), 29.3 ± 4.4 Mg C ha^{-1} a^{-1} (Tapajós) and 31.4 ± 4.4 Mg C ha^{-1} a^{-1} (Caxiuanã). The error bars in these estimates are dominated by the large errors we ascribe to leaf respiration. When these estimates are compared to those from flux towers (Figure 3), the agreement is close at Manaus and Tapajós. This greatly increases confidence in both these approaches. At Caxiuanã, the flux tower estimate is substantially higher, but our estimate is almost identical to the *Fisher et al.* [2007] estimate (31.2 Mg C ha^{-1} a^{-1}) derived from measured photosynthetic parameters and canopy hydrology. This hints the problem may be with the Caxiuanã flux tower, rather than with the "bottom-up" measurements (the Caxiuanã tower is situated 6 km downwind from a very large water body, which generates large-scale circulations, which may complicate flux measurements). The dominant term in ecosystem respiration appears to be leaf respiration, followed by root respiration, stem respiration, and fine litter decomposition, all of roughly equal magnitude. With some caveats, the fairly close agreement between the two approaches (flux towers or ecophysiology, and bottom-up measurements) indicates there are no very large terms missing, such as enhanced respiration from branches, litter decomposition in situ in the canopy, understory respiration, etc. [*Malhi et al.*, 2009].

It is now possible to calculate the ecosystem carbon use efficiency, the fraction of GPP that is allocated to NPP.

$$CUE_{eco} = \frac{NPP}{GPP} = \frac{NPP}{(NPP + R_{auto})} = 1 - \frac{R_{auto}}{GPP}.$$

The values of CUE_{eco} at Caxiuanã (0.32 ± 0.07) are similar to those at Manaus (0.34 ± 0.10), confirming the picture of low carbon use efficiency in old-growth tropical forests suggested by *Chambers et al.* [2004] for Manaus. At Tapajós, however, CUE_{eco} is higher with a mean value of 0.49 ± 0.16, closer to the values reported in many temperate broadleaf forests. Given the large error bars around the CUE estimates, however, the difference is not significant (z test, $p = 0.14$). Fundamentally, this difference reflects the fact that the observations of higher wood and litter production at Tapajós are not matched by a higher GPP as seen by both the flux tower and the sum of "bottom-up" measurements.

Hence, at Tapajós, there is some suggestion of disproportionate allocation to above ground productivity (canopy and woody growth), with a commensurate reduction in metabolic activity such that overall GPP is very similar between the three focal LBA sites. The difference in carbon cycling between Tapajós and the other two sites may therefore primarily reflect differences in allocation rather than differences in photosynthesis. The most plausible hypothesis to explain this difference is that there is likely to have been a significant mortality event in Tapajós in the 1990s [*Pyle et al.*, 2008] and that in the aftermath of the mortality, there is a surge in growth with surviving and newly recruiting individuals competing for increased light availability by allocating disproportionately to wood and canopy production, thus causing an increase in CUE.

7. SPATIAL INTERPOLATION TO THE WIDER AMAZON REGION

The three LBA focal study sites are located in the region associated with some of the least dynamic, slowest-growing forests in Amazonia [*Malhi et al.*, 2009]. The new RAINFOR NPP sites (Figure 4) present part of the first comprehensive multisite assessments of the carbon cycle published for other parts of Amazonia. *Cavaleri et al.* [2008] present a fairly comprehensive assessment for the La Selva forest in Costa Rica.

Plate 1 [from *Malhi et al.*, 2006] presents regional extrapolations of basal area, AG wood productivity, and wood residence time (defined as AG live biomass/stem productivity). A simple extrapolation based on kriging is employed here to indicate general trends; more sophisticated studies using soil maps and/or remote sensing metrics would indicate differences in detail but the same broad trends.

The increase in productivity from east to west is mirrored by a corresponding decrease in biomass residence time (defined as AG woody biomass divided by AG woody productivity). This is the average time that carbon stays fixed in live biomass in an Amazonian forest. The mean residence
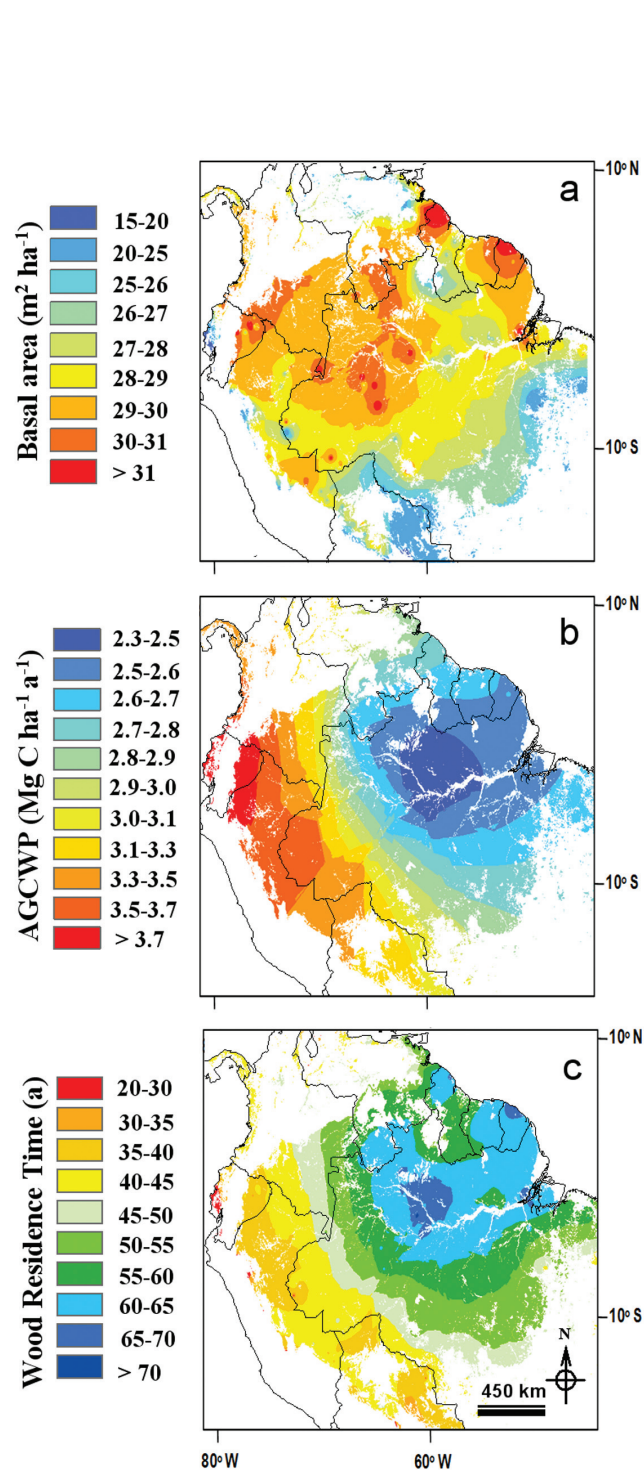
Plate 1. Spatial variation of (a) basal area ($m^2\ ha^{-1}$), (b) AG coarse wood productivity (NPP_{stem} − $Mg\ ha^{-1}\ a^{-1}$) and (c) wood residence time (years) across Amazonia. White areas are outside the boundaries of intact evergreen forest. From *Malhi et al.* [2006], copyright Wiley-Blackwell.
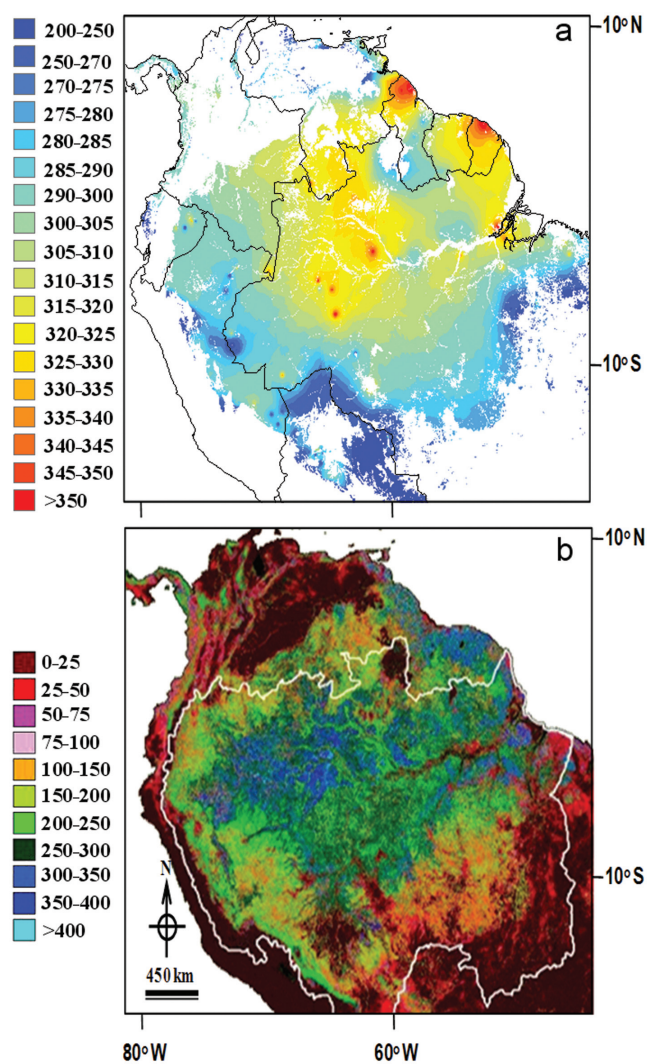
Plate 2. Spatial variation of AG biomass across Amazonia determined by (a) *Malhi et al.* [2006] using geo-statistics and (b) *Saatchi et al.* [2007] using remote sensing. Note that Plate 2b covers a slightly larger area. Units are in Mg dry weight ha^{-1} (1 Mg dry weight ~ 0.5 Mg C).

time in eastern Amazonia is 65–70 years, but declines to 30–40 years in western Amazonia. Our basic extrapolation suggests that the region-wide AG wood productivity of Amazonia is around 1.7 Pg C a^{-1} (per unit area, 2.93 Mg C $ha^{-1}\ a^{-1}$). This number increases by about 21% (to 2.06 Pg C a^{-1}) if BG biomass is taken into account. If we take our estimate of $NPP_{canopy} = 1.61 \times NPP_{stem}$ to be general (Figure 4), the total AG NPP of Amazonian forests is 4.4 Pg C a^{-1}. *Malhi et al.* [2006] use a similar but larger data set to estimate an AG live biomass of 93 ± 23 Pg C a^{-1} (see below).

Dividing the AG biomass by the wood productivity suggests a mean residence time for live woody biomass of 55 years. In conclusion, Amazonian tropical forests incorporate about 2 thousand million tons of carbon in woody biomass each year, which resides in the live biomass for about 55 years.

Two recent regional extrapolations of biomass are compared in Plate 2. Plate 2a plots an inverse-distance-weighting extrapolation based on forest plot data corrected for wood density variation [*Malhi et al.*, 2006]; Plate 2b plots a remote sensing-based extrapolation built from a different, partially overlapping biomass data set [*Saatchi et al.*, 2007]. The interpolation of tree biomass presented by *Malhi et al.* [2006] incorporates in-depth understanding of forest structure and wood density, but relies on relatively crude extrapolation from a few sample points to the wider region. It may identify key regional trends, but is unreliable as a predictor of biomass for any particular region. In particular, *Malhi et al.* [2006] identify some decrease in biomass in the more productive regions, which reflects a decrease in mean wood density and, in turn, reflects a life-history trade-off as faster growing species with low wood densities increase in abundance relative to high wood density, slow-growing species.

As an alternative approach, *Saatchi et al.* [2007] apply multiple remote sensing layers to a (different) biomass data set and utilize a tree-based regression approach and direct estimation techniques to map the AG live biomass of forests at a moderate spatial resolution (1 km) over the entire Amazon basin and surrounding areas. The methodology relies on the sensitivity of the remote sensing measurements to various attributes of forest cover such as canopy roughness and moisture, tree density, leaf area index, crown and stem volume to extrapolate the ground biomass data over the basin, but incorporates less direct ecological understanding of forest composition. These attributes are known to be strongly correlated with the biomass density [*Saatchi et al.*, 2007; *Chambers et al.*, 2007; *Liddell et al.*, 2007; *Alves and Santos*, 2002]. The biomass distribution captured both the large-scale variations of the carbon stores across the Amazonian and finer-scale heterogeneities at the landscape level associated with variations in soil, geomorphology, topography, and moisture gradients.

Both the remote sensing and ecologically derived maps show similar trends with the highest biomass in the northeast and central Amazonia and lower biomass in the west and south. At the large scale, these high-biomass regions correspond to areas with high rainfall and short dry season [*Malhi et al.*, 2006; *Saatchi et al.*, 2007]. At the finer scale, areas of northwest and southwest Amazonia with lower biomass have larger heterogeneity that may be associated with species composition, higher turnover, wood density-basal area

ratio and, to some extent, the soil fertility and topographical variations [*Baker et al.*, 2004; *Saatchi et al.*, 2007]. In total, *Malhi et al.* [2006] estimate an AG live biomass of 93 ± 23 Pg C over a forest area of 5.76×10^6 km² (including a 10% correction for the biomass of small trees and lianas, which are not usually included). *Saatchi et al.* [2007] arrive at a smaller estimate of 66 ± 15 Pg C over an area of 5.46 $\times 10^6$ km². The difference can partially be explained by the inclusion of savanna in the *Saatchi et al.* estimate and by the omission of a 10% correction for small trees and lianas.

A logical next step is to combine both approaches, utilizing the ecological insight from in-depth plot level studies with multiple remote sensing measurements of forest structure, moisture and phenology. One such approach would be to first generate and interpret maps of relevant parameters such as wood density, forest structure (e.g., basal area, height, fraction of large trees) and then build up to a region-wide map of biomass.

8. WHAT CONTROLS THE BIOMASS AND DYNAMISM OF AN AMAZONIAN FOREST?

Figures 3 and 4 highlight that woody production accounts for only a small proportion of the NPP in the three Amazonian forests studied here and an even smaller proportion of the GPP. Hence, it is quite likely that small shifts in carbon allocation can generate large shifts in wood productivity (Figure 4). These shifts may matter more than shifts in photosynthesis in determining spatial and temporal patterns in wood production.

An initial assumption may be that areas of high productivity correspond to areas of high biomass. This is manifestly not the case (Plate 1). An emerging insight is that biomass of old-growth systems seems to be determined less by productivity and more by turnover or residence times. Put another way, for near-equilibrium old-growth forests, the rate of mortality generally increases as wood productivity increases. This suggests that for given environmental conditions, there is some form of cap on the "carrying capacity" of biomass of an old-growth tropical forest. A likely cause of this cap is competition between tree crowns for light resources. A closed tropical forest canopy already captures or reflects almost all of the incident photosynthetically active radiation, and in the absence of changes in incoming solar radiation, increased supply of other limits to productivity is likely to intensify competition for light resources and thereby enhance mortality among those individuals that lose out in light competition. Hence, a stand-level constraint on biomass emerges that cannot easily be identified from understanding response of individual trees to the environment. A boost in productivity thereby induces a boost in mortality in the long-term,

although there may be transient increases in biomass as the system tries to re-equilibrate.

This insight emerges from analysis of spatial patterns of productivity and biomass. When considering changes in the biomass of old-growth forests over time, for instance, in response to rising carbon dioxide considerations, similar constraints may come into play. There may be a short-term increase in biomass, but the long term competition for light may present a stand-level constraint on total biomass. It may be the response of this stand-level constraint to environmental change that determines future changes in the biomass of old-growth forests, rather than individual-level responses in productivity. For example, increased atmospheric CO_2 concentrations may increase water use efficiency, affecting the maximum height of canopy trees. Any stimulation of productivity (whether stimulated by soil fertility over space, or by CO_2 over time) could result in a more dynamic forest with increased abundance of pioneers, lianas, and other disturbance-favoring taxa. The interaction between increasing dynamism, forest structure, and plant traits also have the potential to act as a positive feedback, or ecological "amplifier." As forest mortality rates increase, there may be greater gap frequency in the canopy and greater light penetration to the understory. This will favor fast-growing, short-lifetime species, which further increases mortality and canopy openness. Such discussion is speculative, but highlights our lack of knowledge of the fundamental controls on the biomass of old-growth tropical forests.

In conclusion, intensive LBA research at the three focal sites presented here has painted a comprehensive picture of the allocation of productivity at at least these sites in eastern Amazonia and demonstrated how sensitive the woody biomass growth is to small shifts in carbon allocation priorities within the forest. The RAINFOR project has demonstrated the generally higher productivity of Western Amazonia, but it is still a subject of active research as to whether that higher productivity is driven by increased photosynthesis or by a shift of allocation to woody production. We emerge from a decade of LBA-related research with a fairly comprehensive picture of fine-scale local dynamics at particular sites and a gradually emerging (but far from complete) sense of large-scale regional variations in NPP and carbon cycling. Studies of the contemporary carbon cycle of the Amazon region can now be based more on rich data validation at multiple sites rather than model assumption. These insights have answered some questions and inevitably raised more questions and challenges that will be the focus of another decade of research. We would venture to suggest that many answers to these questions lie in new study sites away from the LBA sites that have been the focus of this chapter. In particular, the barely studied forests of western Amazonia, the floodplains,

the crystalline shield, and the Andes beckon. Our journey toward comprehending the greatest "carbon machine" on the land surface is only just beginning.

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